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Short Communication

Observations of individual humpback whales utilising multiple migratory destinations in the south-western Indian Ocean

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Movements of humpback whales *Megaptera novaeangliae* among breeding regions within the south-western Indian Ocean are poorly understood. Understanding the relationships among breeding regions is critical for effective conservation and management strategies. Through systematic comparisons of molecular genotypes and both systematic and non-systematic comparisons of individual identification photographs collected between 1996 and 2006, we have thus far identified nine whales (six males and three females) utilising two breeding areas within this region: the northern Mozambique Channel and eastern Madagascar. Four of the nine whales were recaptured using only photographic data, two whales were independently recaptured using both photographic and genetic data, and three whales were recaptured exclusively using molecular methods. The discovery of these nine individuals provides much-needed data to guide the formulation and future revision of stock boundaries.

Keywords: conservation, genetics, Indian Ocean sanctuary, mark-recapture, *Megaptera novaeangliae*, microsatellite, migration, photo-identification

Introduction

The south-western Indian Ocean is one of seven major Southern Hemisphere humpback whale *Megaptera novaeangliae* wintering regions currently recognised by the International Whaling Commission (IWC 2000, 2004, 2008). During the austral winter, humpback whales undertake an annual migration from high-latitude feeding regions to low-latitude wintering regions where breeding and calving take place (Dawbin 1966). Best et al. (1998) postulated that there are three principal humpback whale migratory streams within the south-western Indian Ocean: one along the east coast of southern Africa, one along the Madagascar Ridge, and possibly a third through the central Mozambique Channel (Figure 1). These authors stated the possibility, however, that the third migratory stream through the central Mozambique Channel might actually just be wide-ranging animals from coastal Africa and Madagascar.

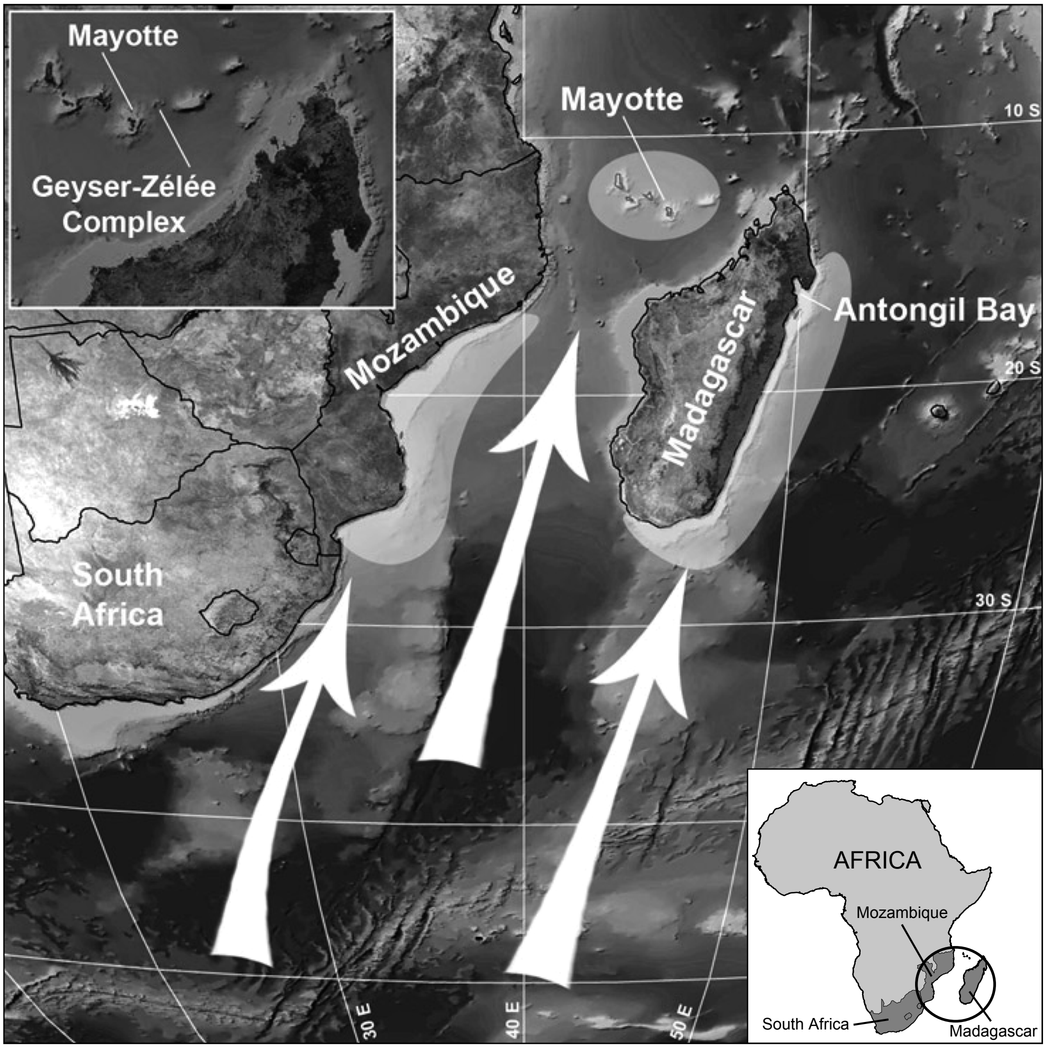

Figure 1: Relationship of sampling sites, migratory routes (white arrows) proposed by Best et al. (1998), and the general extent of the initial south-western Indian Ocean breeding regions (IWC 2000)

With little additional information to support or refute the proposal of three migratory streams, the IWC recognised the termini of these three proposed migratory streams as three separate breeding regions (IWC 2000). The south-western Indian Ocean was collectively identified as Region C and assemblages of humpback whales found among the northern Mozambique Channel Islands (breeding substock C2) were differentiated from assemblages found along the eastern coast of South Africa and Mozambique (C1) and the coast of Madagascar (C3) (IWC 2000). In recent years, the original three breeding regions have been extended and a fourth breeding region has been proposed that encompasses the islands of Réunion and Mauritius (IWC 2008).

Understanding the relationships among breeding regions is critical for effective conservation and management strategies. Through direct evidence of visits to multiple migratory destinations by known individuals, we can better understand the relationship among the breeding assemblages in the south-western Indian Ocean as well as the relevance of the present substock delineations. We present preliminary results from ongoing analyses that have documented nine individual humpback whales utilising breeding areas in both the northern Mozambique Channel and along the eastern coast of Madagascar. Our findings provide much-needed data that can help guide the formulation and future revision of stock boundaries.

Material and methods

Photographic-identification data and skin samples were collected between 1996 and 2006 in both the northern Mozambique Channel and along the eastern coast of Madagascar. Data from the northern Mozambique Channel were collected in the lagoon and surrounding waters of the island of Mayotte (45°10′ E, 12°45′ S) and on the Geyser-Zélée Complex (46°25′ E, 12°24′ S), an offshore reef system between Mayotte and north-western Madagascar (Figure 1). All data from Madagascar used in this analysis were collected in Antongil Bay (49°56′ E, 15°49′ S), located in north-eastern Madagascar.

Humpback whales were photographically identified by examining pigmentation patterns and other natural markings on the ventral side of tail flukes (Katona and Whitehead 1981), as well as the left and right side of the dorsal fin (Blackmer et al. 2000). Tissue samples were obtained through the collection of sloughed skin or by using a crossbow and biopsy dart (Lambertsen 1987). Molecular identification of individuals (Paetkau and Strobeck 1994, Palsbøll et al. 1997) was accomplished by constructing genotypic profiles using 11 microsatellite markers for each sampled animal (genotyping methods described in detail in Pomilla and Rosenbaum 2005).

Results

Between 1995 and 2004, 699 photographs from the northern Mozambique Channel were collected during systematic surveys for humpback whales or were contributed by Service de la Pêche et de l'Environnement Marin and interested whale enthusiasts. During yearly systematic surveys conducted between 1996 and 2006, more than 8 000 photographs of humpback whales were collected in Antongil Bay, Madagascar.

Between 1997 and 2004, 113 tissue samples were collected from humpback whales in the northern Mozambique Channel. Only 94 of these samples were successfully genotyped yielding 80 genetically distinguishable individuals. Over 1 600 tissue samples were collected in Antongil Bay between 1996 and 2006. Of these, 1 526 samples, representing 1 202 genetically distinguishable individuals, were previously genotyped (Pomilla and Rosenbaum 2005, Cerchio et al. 2009) and available for comparison.

Through systematic (i.e. comprehensive and exhaustive) comparisons of the molecular data and both systematic and non-systematic (i.e. opportunistic, non-exhaustive) comparisons of the photographic data, we have identified at least nine whales utilising breeding areas in both the northern Mozambique Channel and eastern Madagascar (Table 1). Four of the nine whales were recaptured using only photographic data, two whales were independently recaptured using both photographic and genetic data, and three whales were recaptured exclusively using molecular methods.

Tissue samples were available for seven out of the nine whales involved in interchanges and were subsequently analysed, using the method developed by Palsbøll et al. (1992), to determine their sex. The remaining two whales were sexed based upon behaviour. Whale MY97-002/AB1030 was engaged in competitive activity at the time of both encounters and is tentatively assigned a sex of male based on its behavioural role, assigned in 2001, of principal escort (Tyack and Whitehead 1983, Baker and Herman 1984, Clapham et al. 1992). Whale AB0440/MY00-024 is presumed to be a female based on the association with a recently born calf during the 2000 encounter. Thus, six of the nine whales were determined to be male and the other three female.

The magnitude of difference in data available for the northern Mozambique Channel and eastern Madagascar reflects the total amount of systematic effort applied in each region. Survey effort in Madagascar consistently covered the majority of the breeding season from July through September, whereas the effort in the northern Mozambique Channel was less consistent and did not cover the main portion of the breeding season for most years. The photographic recaptures reported here are composed of both flukes and dorsal fin identification photographs; however, only fluke photographs have been systematically processed for the 2001 through 2006 Antongil Bay data. Consequently, the photographic recapture by dorsal fin of MY02-026/BA-05-S-043 (Table 1) was made during a non-systematic component of the photographic matching process. Given the temporal consistency noted in individual recapture probabilities for the 2001–2006 Antongil Bay flukes data (Cerchio et al. 2009), it was determined that a standardised assessment of recapture probability was not possible because the sampling periods were not temporally representative and thus yielded non-comparable samples for statistical inference.

Discussion

We have documented the first evidence of exchange of individual humpback whales between eastern Madagascar and the northern Mozambique Channel, two regions that are presently recognised as separate breeding stocks by the IWC. The significance of these findings for population structure, and an accurate understanding of the recovery of this species, must be carefully considered. Interchanges between breeding regions have been previously documented in both the Southern Hemisphere (e.g. Chittleborough 1965, Garrigue et al. 2000, 2002, Pomilla and Rosenbaum 2005) and Northern Hemisphere (e.g. Darling and Jurasz 1983, Darling and McSweeny 1985, Darling and Cerchio 1993, Salden et al. 1999, Calambokidis et al. 2001). It is difficult to interpret the relative significance of the majority of these previously documented interchanges in regards to population structure. Direct comparison and interpretation of previously documented interchanges between breeding regions is hindered by the varying level of effort applied within each region and also because the Northern Hemisphere breeding regions are not delineated or referenced to the same degree as those in the Southern Hemisphere. Interpretation is further complicated by the current definitions and criteria for stocks delineation, which are unclear and poorly documented. Refinement of humpback whale stock definitions has been a major objective of the IWC during the past decade, because early stock boundaries were shown to be not well founded with respect to defining biological units (Donovan 1991).

To date, only a minimal amount of systematic effort has been applied toward understanding humpback whales within the northern Mozambique Channel. Nonetheless, assemblages of humpback whales found in the northern Mozambique Channel and those found along the eastern coast of Madagascar are presumed to be demographically independent and are currently recognised as such, although this assumption has started to be questioned (Pomilla 2005, IWC 2008, Rosenbaum et al. 2009). It is difficult to fully measure the biological (i.e. gene flow) and cultural (i.e. shared behaviours such as song display) impacts of isolated, stochastic interchange events. If interchange events are rare, they should not greatly influence conservation and management decisions. However, there may

Table 1: Dates and locations of encounters with humpback whales observed in both the northern Mozambique Channel and Antongil Bay. Method of recapture indicated in squared brackets under each whale's identifiers

Whale number (sex)	Date	Site	Group type
AB0065/GE-00-S-011 (M)	18 Aug 1996	Antongil Bay	Competitive
[Molecular]	22 Aug 1996	Antongil Bay	Not recorded
	29 Aug 1996	Antongil Bay	Singleton and mother-calf-escort
	21 Jul 1997	Antongil Bay	Pair
	22 Jul 1997	Antongil Bay	Pair
	24 Jul 1997	Antongil Bay	Pair
	02 Aug 1997	Antongil Bay	Singleton and competitive
	03 Aug 1997	Antongil Bay	Competitive
	09 Aug 1998	Antongil Bay	Pair
	11 Aug 1998	Antongil Bay	Pair
	28 Jul 1999	Antongil Bay	Pair
	28 Sep 2000	Geyser-Zélée	Mother-calf-escort
	22 Jul 2005	Antongil Bay	Pair
	06 Aug 2006	Antongil Bay	Mother-calf-escort
AB0203/MY-00-S-002 (M)	02 Aug 1997	Antongil Bay	Pair and competitive
[Molecular]	31 Aug 2000	Mayotte	Not recorded
MY97-002/AB1030 (M?)	21 Sep 1997	Mayotte	Competitive
[Tail flukes]	19 Aug 2001	Antongil Bay	Competitive
MY97-019/AB1073 (F)	01 Oct 1997	Mayotte	Singleton
[Tail flukes and molecular]	14 Sep 2001	Antongil Bay	Singleton
	23 Sep 2002	Mayotte	Singleton
MY98-009/BA-05-S-023 (F)	27 Sep 1998	Mayotte	Singleton
[Molecular]	26 Jul 2005	Antongil Bay	Singleton, competitive and non-competitive
MY98-012/TF-MAD-04-063 (M)	28 Sep 1998	Mayotte	Not recorded
[Tail flukes]	23 Aug 2004	Antongil Bay	Competitive
AB0290/MY04-028 (M)	31 Jul 1998	Antongil Bay	Pair and competitive
[Tail flukes]	29 Jul 2001	Antongil Bay	Pair
	10 Aug 2004	Mayotte	Non-competitive
AB0440/MY00-024 (F)	31 Jul 1999	Antongil Bay	Pair
[Dorsal only]	04 Oct 2000	Mayotte	Mother-calf pair
MY02-026/BA-05-S-043 (M)	07 Sep 2002	Mayotte	Singleton (singer)
[Dorsal and molecular]	24 Sep 2002	Mayotte	Pair
	18 Aug 2005	Antongil Bay	Singleton (singer)
	20 Aug 2005	Antongil Bay	Competitive

be considerable conservation and management implications with a greater degree of interchange that involves larger proportions of each breeding assemblage and/or the character of the interchange is non-random such that subgroups or classes of individuals (e.g. pregnant females) exhibit distinct temporal and spatial movement patterns. This is particularly true for population assessments if they are to be derived independently for each breeding stock (Cerchio et al. 1998, Garrigue et al. 2002).

In the early 1980s, it was postulated that there might be multiple migratory destinations or at least partially isolated subpopulations within the Hawaiian Archipelago (Baker and Herman 1981). It has since been shown, however, that there is considerable movement — within and between years — among the islands of the archipelago by both male and female humpback whales (Cerchio et al. 1998, Mate et al. 1998). The movement within the Hawaiian Archipelago was considered to be sufficient enough to invalidate independent island mark-recapture abundance estimates (Cerchio et al. 1998) and it was recognised that the whole archipelago must be regarded as one region (Calambokidis et al. 2001). A similar scenario was found to exist within the wintering region off the coast of Mexico (Calambokidis et al. 2001).

The shortest path distance between Mayotte and Antongil Bay is approximately 1 000 km, whereas the shortest distance between the land masses is a mere 300 km. Furthermore, the area between Mayotte and Madagascar is characterised by deep channels separating numerous banks and offshore reef systems — the Geyser-Zélée complex being one of them. Given the close proximity of these geophysical features, interchange between eastern Madagascar and areas in the northern Mozambique Channel is not unexpected and the relevance of the present substock demarcations are questioned.

The distances between substock C2 (northern Mozambique Channel) and C3 (eastern Madagascar) are comparable to distances between subareas within the Hawaiian Archipelago or within the west coast of Mexico. We postulate that the interchanges we have documented between the northern Mozambique Channel and eastern Madagascar are analogous to movement within the Hawaiian Archipelago or the wintering region off Mexico. If accurate, our findings would have important implications for delineation of stock boundaries in the south-western Indian Ocean.

Recent broad-scale genetic analyses of Southern Hemisphere humpback whales (Pomilla 2005, Rosenbaum et al. 2009) partially support our current hypothesis. Both studies showed that assemblages of humpback whales sampled in C2 and C3 are not significantly different from each other, but that both C2 and C3 are significantly different from assemblages of humpback whales sampled in C1 (east coast of South Africa and Mozambique). Pomilla's (2005) finer-scale analysis showed, however, that the differentiation observed between C1 and C3 is driven by samples collected off the east coast of South Africa. Samples collected off the coast of Mozambique, while still in C1, were not significantly different from either C2 or C3. While these genetic results support our hypothesis that the C2 and C3 subregions are being utilised by the same humpback whale population, they are insufficient to clearly determine the degree of demographic independence of a hypothetical C2/C3 complex from C1. Based on the findings from these population genetic analyses, a less complete version of the recapture results presented here (Ersts et al. 2006), and the fact that C2 is still considered data-deficient, the IWC grouped C2 and C3 together during the most recent humpback whale population assessment (IWC 2008). However, the C2 and C3 delineation currently still remains.

Whereas all of the recaptures presented here are interannual, we believe that within-season movement is possible but are also formulating a hypothesis that there exist functional differences within wintering regions, such that wintering regions are not uniformly used by subgroups or classes of individuals. In order to fully quantify the demographic independence of substocks in the south-western Indian Ocean, rates of exchange and sighting probabilities, similar to those used to examine data from the Hawaiian Archipelago, are needed. The next step of quantifying exchange rates will require a systematic and dedicated effort to continue and unify data collection in order to equalise effort and synchronise timing of surveys in the two regions. However, as the sighting history for whale AB0065/GE-00-S-011 (Table 1) illustrates, complex movement patterns may only begin to emerge after more than a decade of data collection.

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